

WITHIN-PAIR INTERACTIONS AND PARENTAL BEHAVIOR OF CERULEAN WARBLERS BREEDING IN EASTERN ONTARIO

JENNIFER J. BARG,¹ JASON JONES,^{1,2,4} M. KATHARINE GIRVAN,^{1,3} AND RALEIGH J. ROBERTSON¹

ABSTRACT.—The Cerulean Warbler (*Dendroica cerulea*) is currently the focus of considerable management interest; however, our ability to develop effective management strategies is hampered by a dearth of life history and basic behavioral data. Here, we present information on male-female interactions of Cerulean Warblers and parental nest attentiveness that is, to our knowledge, among the first such rigorously collected data for this species. Males feed females during nest building and on the nest during incubation; the relative infrequency of these events suggests that they play more of a role in pair-bond maintenance than they do in enhancing female energetics. Female incubation rhythms were not significantly influenced by temperature, time of day, or egg age. Compared with other *Dendroica* warblers, we observed relatively infrequent female departures during incubation, perhaps in response to a high risk of nest predation. As the nestlings aged, females spent less time brooding nestlings, presumably to allow for more frequent feeding; however, both males and females exhibited relatively low rates of food delivery compared with other *Dendroica* warblers. Despite the low rates of food delivery, feeding trips were more frequent at successful nests than unsuccessful nests. Our results suggest that Cerulean Warblers are tightly constrained by the competing pressures of predation risk and sufficient food provisioning for nestlings. Received 28 February 2005, accepted 23 February 2006.

Birds that form socially monogamous pairs during the breeding season exhibit various acoustic (Kroodsmas and Miller 1996) and behavioral (Birkhead and Møller 1992) within-pair interactions. These social behaviors can have conservation and management implications; indeed, our ability to manage or conserve species of interest is often unwittingly limited by our poor understanding of basic life history and behavioral phenomena (Komdeur and Deerenberg 1997). Hopefully, the careful documentation of these behaviors will assist us in identifying species' social requirements, which may be used to augment management and conservation strategies based on habitat requirements. The Cerulean Warbler (*Dendroica cerulea*) is a poorly known species of particular concern due to population declines of up to 3% per year since 1966 (North American Breeding Bird Survey data; Robbins et al. 1992, Link and Sauer 2002), probably due to habitat loss in both North America and South America. In the United States, the species has been variously designated as threat-

ened, rare, or of special concern; in Canada, it is a species of special concern (Robbins et al. 1992, Hamel 2000, Committee on the Status of Endangered Wildlife in Canada 2003); and it is listed as vulnerable by the International Union for Conservation of Nature and Natural Resources (2004). However, the design and implementation of effective conservation and management strategies has been slowed by limited availability of life history and behavioral data (Hamel et al. 2004).

As a result of long-term research, beginning in 1994 at the Queen's University Biological Station (QUBS) in Ontario, Canada, we have learned a great deal about habitat selection behavior (Jones et al. 2001; Jones and Robertson 2001; Barg et al. 2005, 2006), reproductive ecology and population dynamics (Oliarnyk and Robertson 1996, Jones et al. 2004), and population structure (Gibb et al. 2005, Jones et al. 2005, Veit et al. 2005) for the enigmatic Cerulean Warbler. Here, we present data on Cerulean Warbler male-female interactions and parental nest attentiveness that is, to our knowledge, among the first such rigorously collected data for this species. Specifically, we were interested in how males and females coordinate reproductive activities, how they divide parental responsibilities, and how patterns of nest attendance were influenced by weather variables, partner behavior, and nesting stage.

¹ Dept. of Biology, Queen's Univ., Kingston, ON K7L 3N6, Canada.

² Current address: Dept. of Biology, Vassar College, Poughkeepsie, NY 12604, USA.

³ Current address: Norval Outdoor School, Box 226, Norval, ON L0P 1K0, Canada.

⁴ Corresponding author; e-mail: jajones@vassar.edu

METHODS

We collected data during the breeding seasons (May–July) of 1999–2001, at QUBS, Lake Opinicon, Leeds/Frontenac counties, Ontario, Canada (44° 30' N, 76° 20' W). The forest there is characterized as second growth deciduous, between 80 and 90 years old. The canopy is dominated by sugar maple (*Acer saccharum*), bitternut hickory (*Carya cordiformis*), and ash (*Fraxinus* spp.); the mid- and understories are primarily hophornbeam (known as ironwood in Canada; *Ostrya virginiana*) and sugar maple saplings. We used microclimate data loggers (Onset HOBO® H8 Pro Series data loggers, Bourne, Massachusetts) to record temperature and relative humidity hourly at two separate locations within the study site, which was a 24-ha area on QUBS property.

Each year, we captured territorial males by using target-netting techniques (whereby a mist net was erected in a male's territory and a conspecific playback and model presentation were placed nearby to attract the male towards the net). We banded all males with unique combinations of color bands and a Canadian Wildlife Service band. Females were more difficult to capture, as they were largely unresponsive to playbacks; thus, we attempted other methods, including chickadee mobbing calls, hoop nets placed at nests, and owl calls with presentations of owl models, to capture females. The few females we did catch (also banded) were captured opportunistically when they were visiting water sources, feeding fledglings low in the canopy, collecting nesting material, or flushed off nests low in the canopy.

The Cerulean Warbler's breeding season in Ontario is approximately 60–75 days. Over the course of our long-term study (1996–2001; 201 nests), we determined that nest building takes 4–7 days, egg laying ≤ 7 days, and incubation 10–12 days; the nestling stage lasts 10–11 days. The female does all the incubating and brooding, and both males and females feed the young. Nests were checked every 2–3 days. Mirrors attached to telescoping poles were used to see into the nests; if a nest could not be reached with the mirrors, we used parental activities, such as departure fre-

quency, food delivery, or fecal sac removal, to assess nesting status.

We classified nests that fledged at least one young as successful. As the high location of nests made it difficult to determine their fates precisely, we combined all unsuccessful nests for analyses, whether they had succumbed to predation, exposure, abandonment, or some unknown cause. We hired a professional tree-climber to access nests during the nestling stages in 2000–2001. On average, it took >3 hr per nest to access and process the nestlings. Mean brood size in the nine nests that we accessed was 3.3 nestlings (range = 3–4).

To document parental behavior and within-pair interactions, we performed a series of focal nest watches in 1999–2001. For each watch, a single observer monitored activity at a nest for 30 min. Female presence or absence at the nest was recorded every minute. The observer also kept a running tally of departure/arrival times, male and female vocalizations, male visits to the nest, and feeding trips made by the male and the female—documenting the food item whenever possible. Given our inability to access most nests, we were not able to calculate provisioning rates on a “per nestling” basis, which would have allowed us to control for any potential effects of brood size on provisioning rates. Nest watches were performed on individual nests at 2- to 3-day intervals until the nestlings fledged or the nest failed; nest status was monitored between watches. Where nest visibility permitted, we videotaped nests for 2-hr periods; this allowed us to assess the bout length of incubation and brooding without the 30-min time constraint of focal-nest watches. To increase our nest-watch sample size, we included the first 30 min of each video recording in our analyses; there were no significant differences in the patterns of incubation and brooding between our focal nest watches and the first 30 min of our video recordings (all $P > 0.20$). No nest was watched or videotaped more than once on any given day.

Analysis.—We used analysis of covariance (ANCOVA) to analyze incubation patterns based on 130 watches (117 direct, 13 video) from 39 nests and 31 females conducted during 1999–2001; this included nests of females that renested ($n = 7$). Fixed effects in the ANCOVA models were time of day and day of

incubation, with ambient temperature included as a covariate. Because we performed multiple watches on each female, "individual" was included in the model as a random effect. To control for seasonal effects (Julian date was significantly correlated with ambient temperature; $r = 0.45$, $P < 0.001$), we regressed time spent incubating per 30-min watch on Julian date and used the residuals from this linear regression as the response variable in the ANCOVA model.

We used ANCOVA to analyze brooding patterns based on 135 watches (111 direct, 24 video) from 40 nests and 35 females during 1999–2001. Fixed effects in the ANCOVA models were time of day and nestling age. As in the incubation models, we included "individual" as a random effect. We conducted separate analyses for two covariates: ambient temperature and male feeding rates. For the temperature model, we used the residuals from a regression of time spent brooding on Julian date as our response variable. For the male-feeding model, the response variable was the time spent brooding per 30-min watch (untransformed). In our analysis of male feeding rates, we only included 2000–2001 data (77 watches, 31 nests, 25 females). We had to exclude 1999 male feeding rate data due to consistent observer bias detected in that year; one field assistant neglected to consistently record whether or not a male was carrying food upon arrival at the nest. We also used ANCOVA models to examine the effect of ambient temperature and male feeding rate on the number of feeding trips made by females. As in the incubation and brooding models, we included "individual" as a random effect. Male feeding rate data were excluded.

We performed *t*-tests to compare time spent incubating and brooding, and the number of feeding trips (per 30-min watch) at successful versus unsuccessful nests. There was no statistically significant difference between the average timing (defined by incubation day) of watches on successful (mean incubation day of watches = 7.3 ± 0.4) and unsuccessful (mean = 7.2 ± 0.4) nests ($t = 0.14$, $df = 128$, $P = 0.89$). In addition to nest success (i.e., whether or not a nest fledged at least one young), we also included an analysis of survival by nesting stage (i.e., whether or not a nest survived the incubation period) because

parental activity during the incubation phase is known to affect nest success (Martin and Ghalambor 1999, Ghalambor and Martin 2002). No nest watches were performed on unsuccessful nests after day 10 of the brooding period; therefore, all watches conducted after day 10 at successful nests were excluded from our analysis of parental behavior. In this restricted data set, there was no statistically significant difference between the average timing (defined by brooding day) of watches on successful (mean brooding day of watches = 5.4 ± 0.4) and unsuccessful (mean = 5.0 ± 0.1) nests ($t = 1.77$, $df = 104$, $P = 0.08$). Data are presented as untransformed means \pm SE. All statistical analyses were performed using JMPIN (ver. 4.0.2; SAS Institute, Inc. 2000).

RESULTS AND DISCUSSION

Reciprocal vocalizations.—We documented 136 instances of reciprocal vocalizations (male vocalization followed immediately by female call) during the study period. In the context of reciprocal vocalizations, males were more likely to sing quiet songs (whisper songs) during nest building than during the other stages of the nesting cycle (nest building: 62% of reciprocal vocalizations; incubation: 18%; brooding: 24%; $\chi^2 = 23.09$, $df = 2$, $P < 0.001$). When females are nest building, males tend to follow very closely (often within 1–2 m) and regularly sing whisper songs directed at the female (JJB pers. obs.). Presumably, this following behavior during the fertile period is a form of mate guarding, while the whisper singing with occasional female response presumably functions in pair-bond maintenance. Our observations of male whisper singing during nest building are similar to John and Kermott's (1991) observations of the House Wren (*Troglodytes aedon*); whisper singing by male House Wrens also may serve to stimulate ovulation in the females (Johnson and Kermott 1991). Interestingly, male Cerulean Warblers would frequently whisper sing while females inspected potential nest sites; males would usually inspect these same sites immediately thereafter (JJB pers. obs.). Males were rarely heard whisper singing away from the female or the nest (Barg et al. 2005). Whisper singing by males in similar

contexts has been observed in other parts of the breeding range (Rogers 2006).

Nearly two-thirds (63%) of the reciprocal observations occurred during the incubation stage, although the function of reciprocal vocalizations while the female is incubating is unclear. One possibility was that male vocalizations signal an "all-clear" for females to leave the nest; however, this was not supported by our data, despite our expectations based on anecdotal observation prior to data collection. The frequency of male whisper songs versus normal songs did not influence whether or not a female stayed on the nest following the reciprocal vocalization (Fisher's exact test, $P = 0.45$). Future research should be designed to test a second possibility, that a female response to a male vocalization may encourage male care (Halkin 1997).

Females regularly chip (without prompting by male song) when departing the nest for an off-bout (approximately 50% of departures; JJB pers. obs.), possibly as a signal to males that the nest is unprotected (e.g., Barber et al. 1998). During a survey of 15 songbird species in which females gave nest-departure calls, McDonald and Greenberg (1991) reported that, unlike the Cerulean Warbler, most of the species inhabit grassy or shrubby habitats and that the calls appear to reduce male activity at the nest, presumably to reduce the risk of predation. Male Cerulean Warblers frequently attended the nest for the duration of the female's off-bout, sitting quietly <2 m from the nest in the nest tree; sometimes the male perched on the edge of the nest but was never observed sitting on the nest (i.e., no incubating or brooding) during our watches. Apparently, males of other species are also known to exhibit nest vigilance during female absences (e.g., Northern Mockingbird, *Mimus polyglottos*; Breitwisch et al. 1989).

Mate feeding and mate quality.—We made 28 observations of males feeding females (i.e., courtship feeding) during nest building. Over half ($n = 15$) of these feeding events were followed by copulations. In all cases, the food item presented was a larval lepidopteran. Thirty-five percent of the males (16 of 46) also were observed feeding incubating females (mean = 0.70 ± 0.06 feedings/hr).

Originally, mate feeding was hypothesized to strengthen pair bonds (Lack 1940) or to

serve as an index of mate quality—thereby influencing future mate choice (Nisbet 1973). More recently, researchers have shown that mate feeding can represent an important nutritive and energetic contribution to the female (Royama 1966; Lyon and Montgomerie 1985, 1987; Hatchwell et al. 1999) and may compensate for poor-quality territories (Lifjeld and Slagsvold 1986). Finally, mate feeding may serve to reduce the incidence of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), presumably by reducing female activity and keeping her on the nest; this advantage, however, may carry the cost of increased nest predation resulting from greater levels of male activity at the nest (Tewksbury et al. 2002).

The hypotheses regarding nutrition and energetics are unlikely candidates for explaining mate feeding among Cerulean Warblers, primarily because their relative frequency of mate feeding is low (less than one visit per observation hr); however, it is not clear how frequent mate feeding must be before it significantly affects female condition. Assessing the potential selection pressure of brood parasitism on mate feeding requires feeding data from nests that were parasitized; however, despite a high density of cowbirds in the region (JJ unpubl. data), we have never observed Cerulean Warbler parents feeding cowbird nestlings or fledglings. Furthermore, since 1994 we have detected cowbird eggs in only two Cerulean Warbler nests, both of which were abandoned.

We have made several observations that offer indirect support for the notion that female Cerulean Warblers are capable of assessing mate quality and potentially basing their mate-choice decisions on those assessments. First, we witnessed extra-pair copulations by banded individuals and, for the two complete families for which we obtained blood samples (on a separate project), >50% (4/7) of young were sired by a male other than the social mate (JJB unpubl. data). The criteria female Cerulean Warblers use to choose extra-pair mates are unknown, but presumably they involve judgments of male quality. Second, we observed an instance of double brooding (i.e., initiation of a second nest following a successful first nest). Double brooding may occur more frequently, but our difficulty in capturing females limits our understanding of certain reproduc-

TABLE 1. Incubation patterns ($n = 130$ focal nest watches) of female Cerulean Warblers at the Queen's University Biological Station, eastern Ontario, 1999–2001, were not affected by time of day, incubation day, or ambient temperature. During the nestling stage ($n = 135$ focal nest watches), females spent less time brooding as nestlings aged. No interactions were statistically significant (all $P > 0.10$) in these ANCOVA models. Boldface values denote significant model effects. The male feeding-rate model is based on 2000–2001 data only.

Source of variation	Mean square	df	<i>F</i>	<i>P</i>
Incubation patterns ($R^2 = 0.38$)				
Time of day	2.03	1	0.24	0.62
Incubation day	9.65	13	1.15	0.32
Ambient temperature (covariate)	11.59	1	1.39	0.24
Individual female	8.29	30	0.99	0.49
Error	8.36	84		
Brooding patterns				
Temperature as covariate ($R^2 = 0.57$)				
Time of day	12.18	1	0.30	0.58
Nestling age	160.84	13	4.02	<0.001
Ambient temperature	11.36	1	0.28	0.60
Individual female	51.63	34	1.29	0.18
Error	40.06	85		
Male feeding rate as covariate ($R^2 = 0.58$)				
Time of day	2.53	1	0.07	0.80
Nestling age	113.67	11	3.00	0.006
Male feeding rate	22.09	1	0.56	0.57
Individual female	35.22	24	0.93	0.57
Error	37.92	39		

tive behaviors. What makes this single observation germane is that this female was the secondary female of a bigamous male, who provided very little parental care to her first brood; once her fledglings were sufficiently mobile, the female moved the brood ~800 m (the width of four territories) and re-mated with a different male (all birds were banded). The female's choice of a second mate appeared to be based on this male's willingness to provide parental care to her fledglings, something not offered by her first mate. This second male "adopted" her brood by feeding the young while the female built a new nest and laid a clutch of five eggs (this second nesting attempt was unsuccessful). Although this is the first documented case of brood adoption in Cerulean Warblers, it has been documented occasionally in other wood warblers (e.g., Hooded Warbler, *Wilsonia citrina*; Evans Ogden and Stutchbury 1994). Interestingly, the double-brooded female's new mate already had an active nest and his primary female was incubating at the time of brood adoption. Bigamy is uncommon but regular

on our study site (~10% of breeding males are bigamous; JJB pers. obs.).

Incubation patterns.—On average, females spent 25.7 ± 0.27 min incubating and made 1.0 ± 0.1 departures (range = 0–2) per 30-min watch. For all females (including those recorded on videotape), the average (continuous) duration of an incubation bout was 32.6 ± 3.5 min. After removing the effect of Julian day, the duration of incubation bouts was not significantly influenced by time of day, incubation day, or ambient temperature (Table 1). We detected no differences in incubation time between successful (i.e., surviving incubation or fledging at least one young) and unsuccessful nests (incubation: $t = 1.19$, $df = 128$, $P = 0.24$; fledging: $t = 0.089$, $df = 128$, $P = 0.93$; Fig. 1A).

Incubating females are faced with two decisions, the outcomes of which largely define incubation rhythms (Reid et al. 1999). The first decision—when to leave—is linked to female energy levels. The second—when to return—is linked to female foraging efficiency. In other words, on-bout duration is linked to

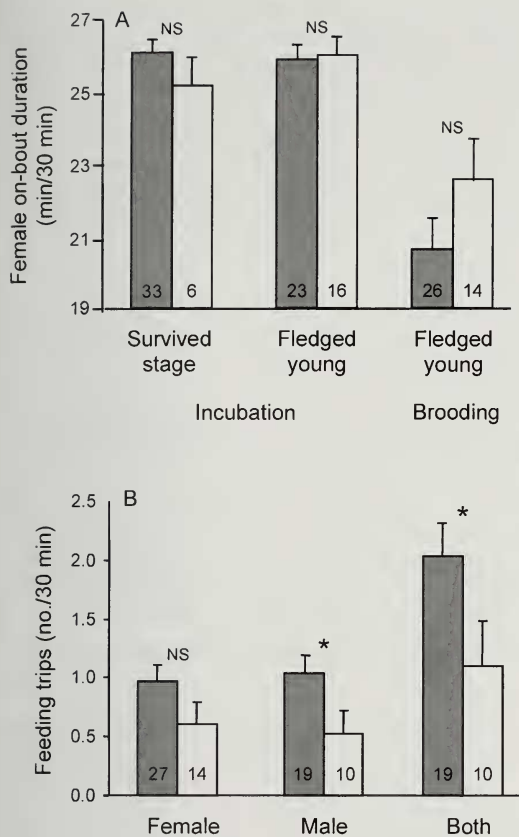


FIG. 1. Cerulean Warbler on-bout duration (A) and feeding behavior (B) for successful (filled bars) and unsuccessful (unfilled bars) nests, Queen's University Biological Station, eastern Ontario. For the incubation period, we defined success in two ways: first, whether or not the clutch hatched, and, second, whether or not at least 1 young fledged from the nest. For the brooding period, success was defined by whether or not at least 1 young fledged from the nest. Data for female on-bout duration and female feeding trips are from 1999 to 2001. Feeding trip data for male and sexes-combined are from 2000 to 2001. Values presented are means \pm 1 SE with sample size inside each column. Brooding sample size is higher than incubation sample size as we included nests that were found after the eggs had hatched. Results of *t*-tests: NS = not significant, * = $P < 0.05$.

parental needs as much as it is to embryonic needs (Conway and Martin 2000a, b). That we detected no significant effect of ambient temperature on incubation patterns implies either (a) that the thermal needs of embryos were met by ambient temperatures (Webb 1987) on our study site, thereby releasing female behavior from this constraint during the day, or

(b) that female behavior was constrained by other pressures, such as female condition, male behavior, or predation risk. Compared with other *Dendroica* warblers (Conway and Martin 2000b), we observed relatively infrequent female departures during incubation (Table 2). Given the lack of a significant relationship between incubation rhythms and temperature, this low frequency of nest departures may be indicative of a high risk of predation (Martin and Ghalambor 1999, Ghalambor and Martin 2002). Nest predation is likely the primary cause of nest failure on our study site (Jones et al. 2001), with Blue Jays (*Cyanocitta cristata*) being the primary predator (JJB pers. obs.); however, given the inaccessibility of most of our nests, we were unable to examine the contents of most abandoned nests to help confirm the cause of failure.

Brooding and feeding young.—Females spent 20.1 ± 7.84 min brooding and made 1.6 ± 0.2 departures (range = 0–3) per 30-min watch. For all females (including those recorded on videotape), the average (continuous) duration of brooding bouts was 16.2 ± 1.5 min. In both brooding models (Table 1), females tended to brood less as nestlings aged, but time of year, temperature, and male feeding rate had no significant effect. We detected no differences in time spent brooding for successful versus unsuccessful nests ($t = 1.63$, $df = 104$, $P = 0.11$; Fig. 1A).

Both males and females averaged 1.1 ± 0.1 feeding trips per 30-min watch (range: females = 0–3, males = 0–4). Females fed more frequently as nestlings aged and as male feeding rate increased (Table 3), corroborating the findings in previous studies (e.g., Nolan 1978, Conrad and Robertson 1993, Lozano and Lemon 1998, MacColl and Hatchwell 2003). Males ($t = 2.40$, $df = 68$, $P = 0.019$) but not females ($t = 0.85$, $df = 93$, $P = 0.40$; Fig. 1B) fed nestlings more often at successful nests than at unsuccessful nests. Adults (both sexes combined) at successful nests made approximately twice as many feeding trips per 30-min watch as they did at unsuccessful nests ($t = 2.12$, $df = 68$, $P = 0.038$; “Both” in Fig. 1B). While we have no direct evidence that differences in food-delivery rates were responsible for differences in nest success, a difference of 1 trip per 30-min watch is larger than it first appears. If we assume a 15-hr day,

TABLE 2. Parental behavior of *Dendroica* wood warblers of northeastern North America. A dash indicates behaviors for which we could find no published information. Very few quantitative estimates of mate feeding are available; therefore, we adopted the qualitative classification of Conway and Martin (2000b).

Species	Nest location	Incubation-bout length (min)	No. incubation departures (hr)	Male incubation feeding	Nestling provisioning rate (nest/hr)	Source
Bay-breasted Warbler (<i>D. castanea</i>)	Tree	18	5.5	Moderate	26	Griscom 1938, Williams 1996
Blackburnian Warbler (<i>D. fusca</i>)	Tree	21–22	4.2	Infrequent	—	Kendeigh 1945, Lawrence 1953, Morse 2004
Blackpoll Warbler (<i>D. striata</i>)	Tree	19	5.0	Moderate	3/nestling/hr	Bent 1953, Hunt and Eliason 1999
Black-throated Blue Warbler (<i>D. caerulescens</i>)	Shrub	20–31	2.9	Moderate	7	Kendeigh 1945, Holmes et al. 2005
Black-throated Green Warbler (<i>D. virens</i>)	Tree	50	1.9	—	12–14	Nice and Nice 1932a, b; Morse and Poole 2005
Cerulean Warbler (<i>D. cerulea</i>)	Tree	33	2.0	Infrequent	3–4	This study
Chestnut-sided Warbler (<i>D. pensylvanica</i>)	Shrub	23	4.5	Moderate	8	Kendeigh 1945, Lawrence 1948, Tate 1970, Richardson and Brauning 1995, Hanski et al. 1996
Magnolia Warbler (<i>D. magnolia</i>)	Tree	17	4.9	—	8	Hall 1994
Yellow Warbler (<i>D. petechia</i>)	Shrub	36	3.1	Frequent	—	Kendeigh 1945, Hanski et al. 1996, Goosen and Sealy 1982, Martin et al. 2000
Yellow-rumped Warbler (<i>D. coronata</i>)	Tree	—	—	—	8–10	Martin et al. 2000, Hunt and Flashpolder 1998

1 caterpillar/trip, 0.1 g/caterpillar, a 10-day nestling period, and 1 extra trip/30 min, parents at successful nests would have delivered approximately 30 g more food to nestlings than unsuccessful parents.

Because increased parental activity late in the nestling stage tends to increase predation risk (Martin et al. 2000), we find it surprising that parents at successful nests made more feeding trips than parents at unsuccessful nests; however, Cerulean Warblers feed nestlings at relatively low rates compared to other passerines (Martin et al. 2000; Table 2), which might lessen the predation resulting from in-

creased activity. Taken together, our observations—male incubation feeding, low rates of female departure, low rates of food delivery, and the possible link between food provisioning and nesting success—suggest that Cerulean Warblers are tightly constrained by the competing pressures of predation risk and food provisioning.

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TABLE 3. Female Cerulean Warblers (temperature ANCOVA: $n = 135$ focal nest watches; male feeding-rate ANCOVA: $n = 77$) at the Queen's University Biological Station, eastern Ontario, 1999–2001, fed nestlings more as nestling aged and as their social mates fed more. No interactions were statistically significant (all $P > 0.10$). Boldface values denote significant model effects. The male feeding-rate model is based on 2000–2001 data only.

Source of variation	Mean square	df	F	P
Temperature as covariate ($R^2 = 0.30$)				
Time of day	0.19	1	0.19	0.67
Nestling age	2.77	12	2.77	0.004
Ambient temperature	0.05	1	0.05	0.82
Individual female	0.23	34	0.23	0.99
Error	1.00	68		
Male feeding rate as covariate ($R^2 = 0.43$)				
Time of day	0.68	1	0.81	0.37
Nestling age	1.68	11	2.01	0.051
Male feeding rate	7.52	1	9.01	0.005
Individual female	0.39	24	0.47	0.98
Error	0.84	39		

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